# The genetic sex-determination system predicts adult sex ratios in tetrapods

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**Adult sex ratio (ASR) has critical effects on behaviour, ecology and population dynamics[1–3], but the causes of variation in ASRs are unclear[4,5]. Here we assess whether the type of genetic sex determination influences ASR using data from 344 species in 117 families of tetrapods. We find that taxa with female heterogamety have a significantly more male-biased ASR (mean proportion of males: 0.55 ± 0.01 SE) than taxa with male heterogamety (0.43 ± 0.01). The genetic sex-determination system explains 24% of interspecific variation in ASR in amphibians and 36% in reptiles. We consider several genetic factors that could contribute to this pattern, including meiotic drive and sex-linked deleterious mutations, but further work is needed to quantify their effects. Regardless of the mechanism, the effects of the genetic sex-determination system on the adult sex ratio are likely to have profound impacts on the demography and social behaviour of tetrapods.**

Adult sex ratio (ASR) varies widely in nature, ranging from populations that are heavily male-biased to ones composed only of adult females[5–8]. Birds and schistosome parasites tend to have male-biased ASR, for example, while mammals and copepods usually exhibit female-biased ASR[5]. Extreme bias occurs among marsupials (Didelphidae and Dasyuridae): males die after the mating season, so there are times when the entire population consists of pregnant females[9]. Understanding the causes and consequences of ASR variation is an important goal in evolutionary biology, population demography and biodiversity conservation because ASR impacts behaviour, breeding systems, and ultimately population fitness[1,2,10–13]. It is also a significant issue in social sciences, human health and economics, since unbalanced ASRs have been linked to violence, rape, mate choice decisions and spread of diseases like HIV[14–16]. The causes of ASR variation in wild populations, however, remain obscure[5,13,17].

One factor that could impact the ASR is the genetic sex-determination system[7,8,18]. Taxa such as mammals and fruit flies have XY sex determination (males are heterogametic), whereas taxa such as birds and butterflies have ZW sex determination (females are heterogametic). Sex-determination systems could affect the ASR in several ways. A skewed ASR might result from an unbalanced sex ratio at birth caused by sex ratio distorters[19]. Alternatively, a biased ASR could develop after birth if sex chromosomes contribute to sex differences in mortality[8,18,20,21]. Differential postnatal mortality is likely to be the main driver of biased ASR in birds and mammals, since birth sex ratios in these classes tend to be balanced[7].

Here we use data from the four major clades of tetrapods (amphibians, reptiles, birds, and mammals) to assess whether adult sex ratios differ between taxa with XY and ZW sex determination (Fig. 1; Supplementary Table 1). While mammals and birds are fixed for XY and ZW sex determination, respectively, reptiles and amphibians provide particularly attractive opportunities for this study since transitions between sex-determination systems have occurred many times within these clades[22,23]. We compiled published data on adult sex ratios in wild populations and their sex-determination systems (Supplementary Table 1). To control for phylogenetic effects, we used phylogenetic generalized least squares (PGLS)[24] to test for differences in ASRs between XY and ZW taxa, and Pagel's discrete method (PDM)[25] to test whether XY and ZWsystems are evolutionarily associated with female-biased and male-biased sex ratios, respectively. Phylogenies were taken from recent molecular studies (see Methods for details).

Both the ASR and the sex-determination system are highly variable across tetrapods (Fig. 1, Supplementary Table 1). We find that ASR and sex determination are correlated. Before controlling for phylogenetic effects, we find that ASRs are significantly more male-biased in species with ZW sex determination than in those with XY sex determination (Fig. 2, Table 1, Extended Data Table 1). Similarly, the proportion of species with male-biased ASRs is greater among ZW than among XY species (Fig. 1, Table 1). These differences are significant within amphibians, within reptiles, and across tetrapods as a whole (Table 1, Extended Data Table 1).

The pattern remains significant after controlling for phylogenetic effects. Both the mean of ASR across species (analyzed using PGLS) and the proportion of species with male-biased sex ratios (analyzed using PDM) are significantly different between XY and ZW systems within amphibians, within reptiles, and across tetrapods as a whole (Table 1, Extended Data Table 1). The effect is strong in clades with variation in sex determination: the type of genetic sex determination explains up to 24% of the interspecific variance in ASR among amphibians and 36% in reptiles (estimated using PGLS, Extended Data Table 2). The results remain significant when we treat three large clades with invariant sex-determination systems as a single datum each (snakes, ZW; birds, ZW; mammals, XY; Extended Data Table 1), when we make different assumptions about branch lengths in the phylogeny (Extended Data Table 2), and when we use arc-sine transformed ASR values and control for variance in sample size (see Methods).

Body size and breeding latitude correlate with life-history traits in many organisms and these traits could affect ASR[26–28]. Sexual size dimorphism is linked to differential sexual selection acting on males and females and thus influences sex-specific mortality, and has

been suggested to drive the evolution of genetic sex-determination systems[29]. Nevertheless, we find that neither body size nor breeding latitude explains the ASR in phylogenetically controlled multi-predictor analyses (Table 2). Sexual size dimorphism is significantly associated with ASR in reptiles and across tetrapods as a whole, but the effect of the genetic sex-determination system remains significant when size dimorphism is included in the analysis (Table 2).

Sex differences in dispersal may also result in biased ASRs. However, dispersal is unlikely to explain the relationship between ASR and sex-determination systems. First, male-biased dispersal is typical in reptiles regardless of sex-determination system (Supplementary Material 1)[30,31]. Second, there is no relationship between ASR and sex bias in dispersal distance in birds (Supplementary Material 1). Finally, the relationship between sex determination and ASR remain significant when the influence of sex-biased dispersal is controlled for in multi-predictor models in tetrapods (Supplementary Material 1).

The sex-determination system may affect the ASR in the directions seen in the data in a number of ways. First, sexual selection can fix mutations that increase male mating success and decrease male survival. They will accumulate on Y but not W chromosomes, and will accumulate more readily on X than Z chromosomes if they tend to be recessive. Second, biased ASRs could result from recessive mutations at loci carried on the X (or Z) but absent from the Y (or W) chromosome since they are not masked in the heterogametic sex (the "unguarded sex chromosome" hypothesis)[7,8,18], and from deleterious mutations carried on the Y (or W) but not on the X (or Z). At loci carried on both sex chromosomes, alleles on the Y (or W) can show partial degeneration[32]. Population genetic models

suggest deleterious mutation pressure alone may not be adequate to explain ASR biases as large as those observed (Supplementary Material 2), but the models do not include factors that could be important, notably degeneration of Y and W chromosomes by genetic drift[32]. A third hypothesis is imperfect dosage compensation, which may be deleterious to the heterogametic sex[33]. Fourth, distorted sex ratios can result from meiotic drive acting on sex chromosomes[34,35]. Drive more often produces female-biased sex ratios in XY systems at birth[36]. There is little data on drive in ZW systems, but if it operates in a symmetric fashion then we expect it to cause male-biased sex ratios. Fifth, Y and W chromosomes might degenerate during the lifespan, for example by telomere shortening or loss of epigenetic marks, more rapidly than X and Z chromosomes. A final possibility is that sex-antagonistic selection acting on sex-linked loci could lead to biased sex ratios, but unlike the preceding hypotheses there does not seem to be a robust prediction about the direction of the ASR bias it will produce (see Supplementary Material 2).

The limited data that are available do not provide clear support for any of these hypotheses, although critical tests are lacking. For instance, the meiotic drive process predicts biased sex ratios at birth. Although a recent comparative analysis in birds suggests that sex ratios at birth are unrelated to biased ASRs[10], offspring sex ratios have not been compared between different sex-determination systems. Additional insight might come from study of dioecious plants with biased sex ratios[37], but their skewed ASR could result from selection on the gametophytic stage that is absent from animals[38]. Evolutionary feedbacks from the ASR to the sex-determination system are also possible: for example, the ASR could influence sexual size dimorphism and sexual conflict, which in turn could trigger transitions in sex determination[29,39,40].

In conclusion, we demonstrate strong and phylogenetically robust associations between genetic sex-determination systems and a demographic property of populations, ASR. Although the mechanisms that drive this association need further theoretical and empirical analyses, the observed pattern is biologically important for two reasons. First, changes in sex-determination systems are expected to have knock-on effects on social behaviour. Theory suggests that ASR affects violence, pair bonds, infidelity and parental care[1,41], and field-based studies support these predictions[4,13,15,16]. For instance, female-biased ASRs co-occur with polygyny and female care, whereas male-biased ASRs tend to co-occur with polyandry and male care in birds[4]. Second, sex-determination systems may have important demographic consequences through skewed birth sex ratios and sex-biased survival. Such biases may not only impact upon the productivity and growth of populations, but also their genetic composition and viability. Further theoretical, experimental, and comparative studies are clearly needed to understand the linkages between sex determination, demography, and social behaviour.

**Methods Summary**

We collected ASR data for 39 amphibian, 67 reptile, 187 bird and 51 mammal species from the literature. When more than one estimate was available for a species we used their mean. Because genetic sex-determination systems of amphibians vary between closely related species[42], we used only those species in which sex determination was characterized at the species level[22,43]. Sex determination is evolutionarily less labile in reptiles, thus we included all species for which sex determination was known either at the family level or, in variable families, at the species level[22,44,45]. Breeding latitude was calculated as the distance from the Equator in latitudinal degrees (averaged if multiple records were

166 available for a species). Sexual dimorphism in body size was calculated as $\log_{10}$(male
167 size) - $\log_{10}$(female size). All data and their sources are given in Supplementary Table 1.
168
169 We controlled for phylogenetic effects in two ways. First, we tested whether ASR bias
170 (female- or male-biased) is evolutionary associated with the type of sex determination
171 using Pagel's discrete method (PDM)[25] as implemented in *BayesTrait*. Second, we tested
172 for differences in ASR with phylogenetic generalized least squares (PGLS)[24] using the R
173 package *caper*[46]. We used recently published phylogenies for amphibians[47], reptiles[48–50],
174 birds[51], and mammals[52,53]. The branching topology between these four major clades was
175 based on recent tetrapod phylogenies[54,55] (Fig. 1).
176
177 We developed simple population genetic models of the effects that deleterious mutation
178 and sex-antagonistic selection can have on the ASR (Supplementary Material 2). The
179 results regarding deleterious mutations reported in the text assume the mutations are
180 largely or entirely recessive and have multiplicative fitness effects across loci, that the loci
181 are in linkage equilibrium, and that selection is strong relative to mutation and drift. The
182 loci are assumed to be fully sex-linked, and those carried on the one type of sex
183 chromosome (e.g. the X) are assumed to have no homologue on the other type (e.g. the Y)
184 that could otherwise mask a deleterious mutation. Fitness effects of mutations in
185 hemizygotes and homozygotes are assumed equal. In our models of sex-antagonistic
186 selection the loci are fully sex-linked and carried on an X or Z chromosome. The models
187 for both deleterious mutation and sex-antagonistic selection are deterministic. They
188 therefore do not account for stochastic processes (such as “Muller’s ratchet”) that are
189 thought important to sex chromosome evolution[32]. It is possible that the conclusions
190 would change qualitatively if the models were extended to include those additional effects.

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**Supplementary Information** is linked to the online version of the paper at

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## Author Contributions

T.S., A.L. and V.B. designed the study. I.P., V.B., P.F.D. and A.L. collected the reptile, amphibian, mammal and bird data, respectively. I.P., V.B. and A.L. conducted the analyses. M.K. developed the population genetic models. All authors wrote the paper.

## Author Information

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335 **Table 1. The effect of the sex-determination system on the adult sex ratio.**

| Taxon | Number of species | Mean ASR | | | | % species with male-biased ASR | | |
|---|---|---|---|---|---|---|---|---|
| | | XY | ZW | *t*-test† | PGLS† | XY | ZW | PDM† |
| Amphibians | 39 | 0.51 | 0.61 | ** | ** | 42.9 | 90.9 | * |
| Reptiles | 67 | 0.45 | 0.57 | *** | *** | 24.2 | 76.5 | * |
| Birds | 187 | -- | 0.55 | -- | -- | -- | 76.5 | -- |
| Mammals | 51 | 0.37 | -- | -- | -- | 9.8 | -- | -- |
| Tetrapods | 344 | 0.43 | 0.55 | *** | *** | 22.3 | 77.2 | *** |

336

337 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, -- no data or not tested

338 †Detailed results of the statistical analyses are presented in Extended Data Table 1.

339 Mean adult sex ratios (ASR, proportion of males in the population), *t*-tests and percentage of
340 species with male-biased ASRs represent species-level statistics and analyses, while
341 phylogenetic generalized least squares (PGLS)[24] and Pagel's discrete method (PDM)[25] were
342 used for phylogenetically corrected analyses of the difference in ASR between XY and ZW
343 species.

**Table 2. The relationships between adult sex ratio, sex-determination system and other factors in phylogenetically corrected multi-predictor analyses.**

| | Amphibians (*n* = 39) | | | Reptiles (*n* = 67) | | | Tetrapods (*n* = 259) | | |
|---|---|---|---|---|---|---|---|---|---|
| | ***b* (± SE)** | ***t*** | ***P*** | ***b* (± SE)** | ***t*** | ***P*** | ***b* (± SE)** | ***t*** | ***P*** |
| Sex-determination system | 0.10 (± 0.03) | 3.38 | 0.002 | 0.10 (± 0.02) | 4.56 | <0.001 | 0.10 (± 0.02) | 5.23 | <0.001 |
| Body size | 0. (± 0) | 1.41 | 0.166 | 0 (± 0) | 0.78 | 0.440 | 0 (± 0) | 0.05 | 0.962 |
| Breeding latitude | 0 (± 0) | 0.13 | 0.898 | 0 (± 0) | 0.04 | 0.966 | 0 (± 0) | 0.24 | 0.811 |
| Sexual size dimorphism | -0.32 (± 0.34) | 0.92 | 0.363 | -0.31 (± 0.15) | 2.17 | 0.034 | -0.38 (± 0.07) | 5.57 | <0.001 |

Results of phylogenetic generalized least squares (PGLS)[24]. Separate models were constructed for amphibians, reptiles and tetrapods, that included ASR as response variable. For sex determination, *b* is the estimated difference in ASR between ZW and XY species.

**Figure 1. Phylogenetic distribution of adult sex ratio (ASR) and genetic sex-determination systems across tetrapods.** Inner band shows the type of sex determination (red: XY, blue: ZW) and the outer band shows the ASR bias for each species included in the study (red: ≤ 0.5, blue: > 0.5). Sample sizes: 39 species for amphibians, 67 species for reptiles, 187 species for birds and 51 species for mammals (see Supplementary Table 1).

**Figure 2. Variation in adult sex ratio as a function of the sex-determination system in amphibians, reptiles, mammals and birds, and tetrapods (all four clades combined).** Central dots and solid whiskers are means ± 1 SE, horizontal bars are medians, and boxes and dashed whiskers show the interquartile ranges and data ranges, respectively, based on species values. Numbers of species are at the bottom of each panel. See Table 1 and Extended Data Table 1 for statistical results and Extended Data Figure 1 for phylogenetically corrected graphs.

366 **Methods**

367 **Data collection**

368 We collected data on ASR (proportion of males in the adult population) in amphibians and
369 reptiles from literature published by December 2013, by searching in Google Scholar and
370 Web of Science with the key words "sex ratio" and "reptile" or "amphibian" or the scientific
371 names of species. We also used reviews to identify additional data sources[43,56]. ASR data for
372 mammals[7] were obtained from a similar search finished in 2007; and we used avian ASR
373 estimates from our existing data set (Supplementary Information of Liker et al.[13]).
374
375 We specifically collected ASR data for amphibians and reptiles from studies that aimed to
376 obtain representative estimates for the population composition and thus provide reliable sex
377 ratio data[57]. These include either long-term demographic studies applying mark-recapture or
378 sacrificing methods (i.e. each individual was counted only once) with similar capture
379 probabilities for the sexes, or total population counts. When more than one measure was
380 available, we used the total counts of individually marked animals over the study period
381 because this may best approximate the overall ASR. We excluded studies in which the
382 authors explicitly stated or speculated that their data may not represent the population-level
383 ASR, or when the methods were not described in enough detail to assess the reliability of the
384 ASR estimate. Moreover, we tested whether ASR estimates differ between sampling (hand-
385 capture, trap, other) and marking (mark-recapture, sacrifice) methods, and we found no such
386 differences (linear mixed-effects model with species as random factor, sampling: $F_{(3, 105)}$ =
387 0.50, $P = 0.683$; marking: $F_{(2, 105)} = 2.18$, $P = 0.118$; n = 234 records). When more than one
388 estimate of ASR was available for the same population (e.g. from several yearly counts at the
389 same location) we took their mean weighted by sample size. When more than one
390 independent record was available for a species from different populations or studies, we used

391 their simple mean. Weighted and non-weighted mean ASRs were highly correlated
392 (amphibians: Pearson's r = 0.973, $P < 0.001$, n = 35 species; reptiles: r = 0.995, $P < 0.001$, n =
393 60 species); we used non-weighted averages because not all studies reported sample size.
394
395 We categorized the genetic sex-determination (GSD) systems of the species from published
396 sources either as male-heterogametic (XY) or female-heterogametic (ZW). For amphibians,
397 only species with known GSD system were included[22,43], because GSD is an evolutionarily
398 labile trait in amphibians; species within a genus or even populations within a species can
399 differ in GSD[42]. For reptiles, we included all species for which GSD was known either at the
400 family level, or at the species level if both XY and ZW systems were reported in the
401 family[22,44,45]. Our result for reptiles is not changed qualitatively by restricting our analyses to
402 those species for which GSD is known at species level[22], i.e. when species for which we
403 assumed GSD based on other species in the family were excluded (difference between XY
404 and ZW reptile species, phylogenetic generalized least squares model (PGLS)[24,58]: b ± SE =
405 0.11 ± 0.02; t = 4.70, $P < 0.001$, n = 26; $R^2 = 0.479$). All birds were assigned to ZW, and all
406 mammals to XY sex-determination systems[22].
407
408 We also collected data on three additional ecological and behavioural variables to control for
409 their known correlation with ASR and so reduce potential confounding effects in multi-
410 predictor analyses. First, we used body size (in mm) which was measured as snout to vent
411 length for amphibians and squamates, and carapace length for the two turtle species, where
412 possible from the same population for which ASR was reported. Head-body length was used
413 for mammals (n = 36)[59]. Since head-body length is not available for the vast majority of birds,
414 we calculated this from the total body length by extracting bill and tail length (n = 133;

415 Supplementary Table 1). Where we had sex-specific data, the mean of male and female head-
416 body length was used as body size variable in the analyses.
417
418 Second, we estimated sexual size dimorphism (SSD) as $\log_{10}$(male body size) - $\log_{10}$(female
419 body size). For birds, we used body mass dimorphism (data available for n =181 species)[60]
420 due to the lack of sex-specific body length data. The results of the multivariate PGLS model
421 of tetrapods presented in Table 2 remain qualitatively the same when wing length dimorphism
422 (data available for n =153 species) is used for birds instead of body mass dimorphism (effect
423 of sex determination: b ± SE = -0.10 ± 0.02, t = 4.97, $P < 0.001$; body size: b ± SE = 0 ± 0, t =
424 0.06, $P = 0.949$; latitude: b ± SE = 0 ± 0, t = 0.223, $P = 0.823$; size dimorphism: b ± SE = -
425 0.52 ± 0.12, t = 4.33, $P < 0.001$; n = 248 species).
426
427 Third, we included breeding latitude as the geographic coordinates of the ASR studies for
428 amphibians and reptiles, taking absolute values to represent distance from the Equator in
429 latitudinal degree. When the authors did not report latitude, we used Google Earth to estimate
430 it on the basis of the description of the study site. For birds and mammals, we used the
431 latitudinal midpoint of the breeding range of the species (n = 182 and 44 species, for birds and
432 mammals, respectively; sources: V. Remes, A. Liker, R. Freckleton and T. Székely
433 unpublished data for birds, and the PanTHERIA database for mammals[61], respectively). Mean
434 values of these variables were used if multiple data of body size, latitude or size dimorphism
435 per species were available.
436
437 Other possible confounding factors include the lifespan of individuals and sex-specific
438 dispersal distances. First, longer average lifespan may lead to exaggeration of ASR bias.
439 However, in species with available data[62], lifespan is unrelated to ASR (PGLS, birds: b ± SE

= 0 ± 0, t = 0.196, $P$ = 0.845, n = 71 species; mammals: b ± SE = 0 ± 0, t = 0.751, $P$ = 0.457, n = 35 species) and also to the absolute deviation of ASR from 0.5 (i.e. when assuming that longer lifespan can exaggerate ASR bias in either direction; birds: b ± SE = 0 ± 0, t = 1.543, $P$ = 0.127, n = 71 species; mammals: b ± SE = 0 ± 0, t = 0.180, $P$ = 0.858, n = 35 species). Second, sex-specific dispersal can bias ASR due to the higher mortality in the sex with longer dispersal distances. However, we found no evidence of a relationship of sex bias in dispersal either with GSD in reptiles, or with ASR in birds (Supplementary Material 1). For these reasons, as well as because data on lifespan and/or sex-specific dispersal are not available for most species in our ASR data set, we did not include these variables in the main multi-predictor models (see Supplementary Material 1 for additional models including dispersal).

Our final dataset comprises data on 39 amphibian species and 67 reptile species (in total n = 229 ASR records from different populations), 187 bird species and 51 mammalian species (a total of 344 species). We could not find body size and latitude data for some species, thus sample sizes were reduced in multi-predictor models. All species-level data and their sources are given in Supplementary Table 1.

**Data analysis**

To assess the reliability of the amphibian and reptile ASR estimates, we calculated the repeatability of ASR as the intraclass correlation coefficient (ICC) following Lessells & Boag[63], using only those species for which we had at least two ASR estimates from different populations. These analyses show a moderate repeatability of ASR, and that a significant part of ASR variation is interspecific (amphibians: ICC = 0.559, $F_{(22,96)}$= 7.27, $P$ < 0.001, n = 23 species, n = 120 records; reptiles: ICC = 0.524, $F_{(13,26)}$= 4.11, $P$ = 0.001, n = 14 species, n = 40 records). For birds, our earlier analyses showed that nearly half (44%) of the ASR

variation was interspecific, and that the direction of ASR (i.e. male- or female-biased) was highly conserved: in 44 species out 55 (80%), the direction of ASR bias was the same for all repeated estimates[5]. For mammals, we did not find enough multiple ASR data within species to estimate repeatability.

In the comparative analyses we used the topology of Pyron & Wiens[47] for amphibians, a composite phylogeny for reptiles[48–50], Jetz et al.[51] for birds[13], the family-level relationships of Meredith et al.[52] and the genus/species level relationships of Fritz et al.[53] for mammals. For analyses across tetrapods, the branching topology between these four major clades was based on recent tetrapod phylogenies[54,55] (Fig. 1). Since we did not have branch length information for these composite phylogenies, we ran the analyses using arbitrary gradual branch lengths according to Nee's method[64]. However, our results remained consistent when we repeated the analyses with other branch length assumptions (Pagel's method and unit branch lengths[64]; Extended Data Table 2).

To test the association between ASR bias (male- versus female-biased) and GSD (XY versus ZW) in phylogenetically corrected analyses, we used Pagel's discrete method[25] as implemented in *BayesTrait*[65]. We used maximum likelihood methods to fit independent and dependent models for transitions in ASR bias and GSD states, and compared the fit of these two models by a likelihood ratio test[25]. To test the ASR difference between XY and ZW species, we used PGLS models with maximum likelihood estimates of Pagel's lambda values[24] using the R[66] package *caper*[46, 58]. ASR was the response variable in all models, and genetic sex-determination system was fitted as the predictor (Table 1, Extended Data Table 1). The parameter estimate *b* shows the difference in ASR (proportion of males in the population) between ZW and XY species. To test the robustness of the bivariate results, we

490 added body size, breeding latitude and SSD as predictors in multi-predictor models to control
491 for their potential confounding effects (Table 2). As in earlier ASR studies[5,7], the distribution
492 of ASR values did not deviate significantly from normal in the four clades separately as well
493 as in tetrapods as a whole; our results remain qualitatively identical when ASR is arc-sine
494 transformed before PGLS analyses (amphibians: b ± SE = 0.10 ± 0.03, $t_{37} = 3.44$, $P = 0.001$, n
495 = 39; reptiles: b ± SE = 0.12 ± 0.02, $t_{65} = 5.95$, $P < 0.001$, n = 67; tetrapods: b ± SE = 0.11 ±
496 0.02, $t_{342} = 5.24$, $P < 0.001$, n = 344).
497
498 The difference between XY and ZW systems for tetrapods is not sensitive to the inclusion of
499 large clades with uniform sex-determination systems (snakes and birds are all ZW, mammals
500 are all XY) since it remains unchanged when each of these clades is reduced to a single datum
501 of its mean ASR (PGLS: b ± SE= 0.10 ± 0.02, t = 5.07, $P < 0.001$, $R^2 = 0.232$, n = 87).
502 Furthermore, our result is also robust to between-species differences in sample size: when we
503 added log(no. individuals) to the previous model, the effect of sex determination remained
504 significant (b ± SE = 0.15 ± 0.07, t = 2.08, $P = 0.041$) while sample size had no significant
505 effect on ASR (b ± SE = 0 ± 0.01, t = 0.35, $P = 0.72$, n = 78). Furthermore, sample size was
506 not a significant predictor of ASR when we added it as a fourth confounding variable in the
507 full PGLS model (b ± SE = 0 ± 0.01, t = 1.16, $P = 0.250$, n = 78), and the effect of other
508 predictors remained qualitatively the same as in Table 2. Finally, the results do not change
509 when we only used the most reliable ASR data (based on mark-recapture or sacrifice
510 methods): sex-determination system is significantly related to ASR in amphibians, reptiles
511 and tetrapods (PGLS results, amphibians: b ± SE = 0.09 ± 0.03, t = 3.07, $P = 0.004$, n = 35
512 species; reptiles: b ± SE = 0.11 ± 0.03, t = 3.974, $P < 0.001$, n = 22; tetrapods with snakes,
513 birds and mammals included as single data points: b ± SE = 0.10 ± 0.02, t = 4.23, $P < 0.001$, n
514 = 55).

## Population genetic models

We developed population genetic models of the effects that deleterious mutation and sex-antagonistic selection might have on the ASR (Supplementary Material 2). The models assume that deleterious mutations are largely or entirely recessive, that they have multiplicative fitness effects across loci, that the loci are fully sex-linked and in linkage equilibrium, that mutation is not sex-biased, and that selection is strong relative to mutation and drift. Fitness effects of mutations in hemizygotes and homozygotes are assumed equal. Full details of the models are given in Supplementary Material 2. Here we summarize key results.

When deleterious alleles reach a mutation-selection balance, with X-Y sex determination the mean viability of males relative to females is

$$\overline{W}_m \approx \exp\{-3U_X - U_Y\},$$

where $U_X$ and $U_Y$ are the total rates of mutation to deleterious alleles across all loci on the X and Y chromosomes. With Z-W sex determination, the mean viability of females to males is

$$\overline{W}_f \approx \exp\{-3U_Z - U_W\},$$

where $U_Z$ and $U_W$ are the total rates of mutation to deleterious alleles across all loci on the Z and W chromosomes. Using very rough estimates for rates of deleterious mutations appropriate for human sex chromosomes, we estimate that mutation-selection balance might bias the ASR by a few percent. This degree of bias is substantially less than what is

seen in our data. We emphasize that the conclusion could be quite different using other parameter values, or if the model was extended to include stochastic effects.

The second hypothesis to explain biased ASRs that we explored with models is sex-antagonistic selection, the situation in which alleles are selected differently in females and males[67]. In Supplementary Material 2, we use numerical examples to show that under both XY and ZW sex determination, either a female-biased or male-biased ASR can result. Thus there does not seem to be a robust generalization about how sex-antagonistic selection will bias the ASR.

## Methods References


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576 **Extended Data titles and legends**

577

578 **Extended Data Table 1. Detailed analyses of the effect of sex-determination system**
579 **on the adult sex ratio.**

580 These are extensions of Table 1 in the text showing details of the phylogenetically
581 uncorrected (t-tests) and phylogenetically corrected analyses (PGLS[24] and PDM[25]). Birds and
582 mammals were not tested with phylogenetic control because there is no variation in the type
583 of sex-determination system within birds and mammals.

584

585 **Extended Data Table2. Phylogenetically controlled analyses of the relationship**
586 **between adult sex ratio and genetic sex-determination system using different branch**
587 **length assumptions.**

588 These are results of phylogenetic generalized least squares models (PGLS)[24] as implemented
589 in the R package 'caper'[46]. The models assume gradual branch lengths calculated either by
590 Nee's or by Pagel's method, or unit branch lengths[61].

591

592 **Extended Data Figure 1. Phylogenetically corrected mean and standard error of adult**
593 **sex ratio in clades with different sex-determination systems.**

594 Parameter estimates for means and the associated standard errors were calculated by
595 phylogenetic generalized least squares models (PGLS)[24] presented in Extended Data Table 2
596 (with branch lengths estimated by Nee's method).